

**Research article**

## **Nesting and food resources of syntopic species of the ant genus *Polyrhachis* (Hymenoptera, Formicidae) in West-Malaysia**

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### **Summary**

*Polyrhachis* is one of the largest ant genera in the world distributed in the Old World tropics and subtropics. We investigated the nesting and nutrition habits of 10 syntopic species of *Polyrhachis* in West-Malaysia. Striking differences between these species exist in regard to the nesting habits. Our research revealed four different nest types (soil nests, nests in preformed cavities, nests constructed of dead vegetative and soil particles, silk nests). The utilization of silk for nest construction expands the nest diversity of *Polyrhachis* considerably (nests in preformed cavities with silk supplement, pure silk nests, silk nests reinforced by dead vegetative and soil particles).

In regard to nutrition habits of *Polyrhachis* two major modes were found: The tending of trophobionts and the opportunistic exploitation of sugary resources. The trophobiotic species keep their trophobionts inside the nest, inside pavilions, openly exposed and guarded or not guarded by the workers. Species of this group are characterized by large colonies and highly efficient recruitment systems. They defend food sites and sometimes establish territories. The non-trophobiotic species have small colonies, mostly less efficient recruitment systems and do not establish territories or defend food sites. Thus in the genus *Polyrhachis* nesting habits as well as nutrition habits seem to be key factors allowing the coexistence of so many different species.

### **Introduction**

*Polyrhachis* is one of the largest ant genera in the world distributed in the Old World tropics and subtropics. Currently 460 species have been described (Dorow, 1995). Although many species are common, only very few investigations have dealt with the ecological and behavioral diversity of *Polyrhachis* (e.g., Dejean et al., 1994; Dorow and Maschwitz, 1990; Lenoir and Dejean, 1994). The architecture of *Poly-*

*rhachis* nests, in contrast, has attracted the attention of several authors (e.g., Forel, 1892; Karawajew, 1906; Jacobson, 1908). Many species are able to construct silk nests with the aid of their larvae. Pure silk nests (Karawajew, 1906; Jacobson, 1908; Dorow et al., 1990; Maschwitz and Dorow, 1993) as well as silk nests combined with various vegetative matter are found (Forel, 1892; Hölldobler and Wilson, 1983; Takamine, 1983; Yamauchi et al., 1987). But there are also a number of species which build their nests without any larval silk. Collart (1932) described nests constructed of spider silk and various other organic materials. Some *Polyrhachis* species occupy preformed cavities (e.g., Forel, 1892) or nest in the soil.

We studied the nesting habits, the food resources and other parameters of 10 syntopic species of *Polyrhachis* in West-Malaysia. Can nest site differentiation sufficiently explain the diversity of these species? Or are other factors, e.g., the partitioning of food resources, the colony structure, activity rhythms or recruitment systems of comparable importance?

## Material and methods

The study was carried out at the Ulu Gombak Field Studies Centre, which is situated in a secondary lowland dipterocarp forest 30 km NE of Kuala Lumpur, Malaysia. The following niche dimensions were analyzed in our field studies: 1) the nesting habits (nest material, nest sites, nest construction), 2) the distribution of nesting resources in the habitat, 3) the colony structure: colony size, queen numbers and nest numbers. The latter was checked by employing confrontation tests: three ants of each nest were marked and displaced onto a neighboring nest (and vice versa). If hostile interactions occur, the nests we considered to belong to different colonies. As control for possible effects caused by the markings marked ants were released on their home nest. 4) the nutrition habits, 5) the partitioning of food resources (foraging activity, specialization), 6) the food recruitment systems.

The investigation was carried out on 10 *Polyrhachis* species belonging to three subgenera: subgenus *Myrmhopla*: *Polyrhachis arachne* Emery, 1896; *P. bicolor* Smith, 1858; *P. dives* Smith, 1857; *P. furcata* Smith, 1858; *P. muelleri* Forel, 1893; *P. schellerichae* Dorow, 1996; subgenus *Myrma*: *P. illaudata* Walker, 1959; *P. nigropilosa* Mayr, 1872; *P. proxima* Roger, 1863 and subgenus *Polyrhachis*: *P. bellicosa* Smith, 1859.

## Results

### *Nesting habits and nest distribution*

The 10 *Polyrhachis* species show a large diversity in nesting habits. They construct nests in all strata, from the soil up to the forest canopy. Our research revealed four different nest types (Table 1.):

**Table 1.** Nesting habits of 10 selected *Polyrhachis* species, sorted by nest type

Species	Nest type	Nest location	Colonized stratum
<i>P. (Myrma) proxima</i>	soil nests without silk supplement	soil	in the soil
<i>P. (Polyrhachis) bellicosa</i>	nests constructed of dead plant and soil particles without silk supplement	between grass, herbs, dry leaves	on the ground, in the herb and shrub layer
<i>P. (Myrma) illaudata</i>	nests in preformed cavities without silk supplement	cavities in dead and living wood, soil cavities	on the ground, in the herb and shrub layer
<i>P. (Myrma) nigropilosa</i>	nests in preformed cavities without silk supplement	old bamboo culms, preformed soil cavities	on the ground, in the herb layer
<i>P. (Myrmhopla) schellerichae</i>	nests in preformed cavities without silk supplement <sup>1</sup>	only culms of giant bamboo species	all strata, but not on the ground
<i>P. (Myrmhopla) arachne</i>	nests in preformed cavities with silk supplement <sup>2</sup>	only culms of giant bamboo species	all strata, but not on the ground
<i>P. (Myrmhopla) di es</i>	silk nests reinforced by dead plant and soil particles <sup>3</sup>	between leaves, grass, herbs, between twigs	on the ground, in the herb and shrub layer, tree layer
<i>P. (Myrmhopla) furcata</i>	silk nests reinforced by dead plant and soil particles	between/below leaves, between twigs	shrub and tree layer
<i>P. (Myrmhopla) bicolor</i>	pure silk nests <sup>4</sup>	between leaves, in folded leaves	shrub and tree layer
<i>P. (Myrmhopla) muelleri</i>	pure silk nests <sup>5</sup>	under the leaf surface of broad-leaved plants	shrub layer

<sup>1</sup> Schellerich-Kaaden et al. (1997).<sup>2</sup> Dorow and Maschwitz (1990).<sup>3</sup> Wasmann (1905).<sup>4</sup> Jacobson (1908).<sup>5</sup> Karawajew (1906).

## 1. Soil nests without silk supplement

Of the 10 investigated *Polyrhachis* species, *P. (Myrma) proxima* is the only representative nesting exclusively in the soil and digging its own cavities. The nine nests we investigated in detail, were constructed without silk supplements and consisted of a simple tunnel leading into a nest chamber. All nests had one entrance surrounded by a mound of excavated soil (Fig. 1 A). The nest chambers were 12–36 cm deep in the ground (mean 24.7 cm, median 24 cm). Seven chambers could be measured. They were 4–11 cm wide (mean 7.1 cm, median 7 cm), 4–10 cm deep (mean 6.0 cm, median 5 cm) and 3–9 cm high (mean 6.1 cm, median 6 cm). The brood was lying on the chamber floors and there was a “kitchen” midden in one part of each nest chamber.

## 2. Nests constructed of dead plant and soil particles without silk supplement

*P. (Polyrhachis) bellicosa* builds its nests with dead plant matter, sometimes mixed with soil particles, but without silk supplement. We found three nests each of the

size of a human head located directly on the ground between grass and shrubs. The nests were constructed with dry grass particles and propped up by stems of weeds and low shrubs (Fig. 1B). The nests had many entrances. The brood was lying on the ground and was not fixed anywhere with larval silk. A fourth nest was located in the shrub layer, 19 cm above the ground. This nest had been constructed with soil and detritus particles placed between dry leaves. No silk reinforced the loosely arranged material. The four measured nests of *P. bellicosa* were 12.5–32.5 cm in width (mean 22.6 cm, median 22.8 cm), 12.0–22.0 cm in depth (mean 18.0 cm, median 19.0 cm) and 10.0–22.5 cm in height (mean 17.5 cm, median 18.8 cm).

### 3. Nests in preformed cavities

#### 3.1. Nests in preformed cavities without silk supplement

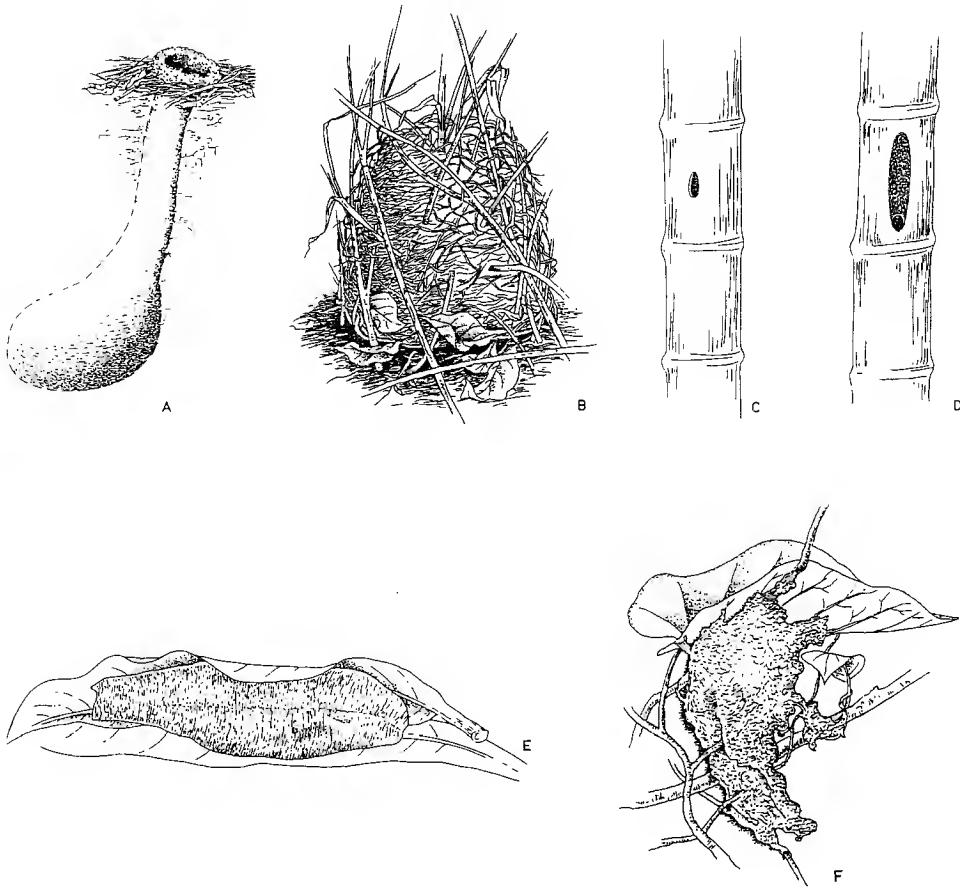
*P. (Myrma) illandata*, a sibling species of the soil nesting *P. proxima*, nests in preformed cavities. *P. illandata* uses no silk for nest construction. The colonies of that species inhabit cavities in living or dead wood, including dead twigs, and abandoned soil nests of other ant species, such as *Diacamma* sp. The 28 investigated nests were either located directly on the ground or in the herb- and shrub layer up to 1.2 m above the ground (mean 0.2 m, median 0.2 m). Of 18 nests measured, the size of the nest chambers varied considerably, ranging from 8.2–69.0 cm in width (mean 35.5 cm, median 33.0 cm), 0.7–8.5 cm in depth (mean 3.3 cm, median 3.5 cm) and 0.7–8.5 cm in height (mean 3.5 cm, median 2.8 cm).

*P. (Myrma) nigropilosa* also nests in preformed cavities without any silk supplement. 24 nests were found in dead bamboo culms lying on the ground or hanging in the vegetation up to 0.65 m above the ground (mean 0.08 m, median 0 m). Only one nest was located in the soil. The bamboo culms either had preformed entrance holes of variable size or the ants were nesting in broken stems. *P. nigropilosa* is able to close big openings with detritus particles. The material is not fixed with silk and therefore not very firm. 24 bamboo nests were measured with a length of 3.0–65.0 cm (mean 34.3 cm, median 33.3 cm) and an inner diameter of 2.3–7.5 cm (mean 4.8 cm, median 5.2 cm). Larvae and pupae were lying on the floor of the nest.

*P. (Myrmhopla) schellerichae* nests exclusively in culms of giant bamboo species (e.g., *Gigantochloa levis*), indicating a specialization in its nesting preferences (Schellerich-Kaaden et al., 1997). The species does not use any silk for nest construction. The ants occupy only culms with preformed small openings (e.g., made by woodpeckers or beetles) excluding larger animals (Fig. 1C). Internodes at any height of living bamboo stems were colonized. The nests were generally confined to one internode each, as the ants are not able to perforate the node. Schellerich-Kaaden et al. (1997) measured 27 nests with a length of 21.5–58.0 cm (mean 41.7 cm) and an inner diameter of 3.2–10.3 cm (mean 8.1 cm). Larval silk is used to attach the brood to the internode walls.

#### 3.2. Nests in preformed cavities with silk supplement

Like *P. schellerichae*, *P. (Myrmhopla) arachne* shows an one-sided plant-host-specialization (Dorow and Maschwitz, 1990). *P. arachne* also nests exclusively in



**Figure 1.** Nesting habits of selected *Polyrhachis* species: (A) soil nest without silk supplement (*P. proxima*), (B) nest constructed of dead plant and soil particles without silk supplement (*P. bellicosa*), (C) nest in preformed cavity without silk supplement (*P. schellerichae*), (D) nest in preformed cavity with silk supplement (*P. arachne*), (E) pure silk nest (*P. bicolor*), (F) silk nest reinforced by dead plant and soil particles (*P. furcata*)

culms of giant bamboo species (e.g., *Gigantochloa scortechinii*, *G. levis*). The ants occupy internodes of living and dead bamboo stems in all positions and heights except for stems lying on the ground. Like *P. schellerichae*, *P. arachne* is not able to perforate the node, so the nests are usually restricted to one internode. But the species occupy adjacent internodes, when these have preformed entrances. The inner nest surface is lined with a silk layer to which the brood is attached. *P. arachne* is able to narrow the preformed entrance openings with a mixture of silk and detritus (Fig. 1D). The species is therefore not restricted to culms with small openings. Five internodes were measured, they had a length of 36.7–48.1 cm (mean 42.5 cm, median 42.6 cm) and an inner diameter of 4.0–9.9 cm (mean 6.5 cm, median 7.1 cm).

#### 4. Silk nests

##### 4.1. Silk nests reinforced by dead plant and soil particles

*P. (Myrmhopla) dives* constructs nests with the aid of larval silk reinforced by dead plant and soil particles (Wasmann, 1905). The shape of these nests varies. We found ball-shaped nests up to human head-size but also flat nest forms. The 13 investigated nests were located either directly on the ground between grass and shrub stalks or up to 1 m above the ground between stalks, leaves or twigs (mean 0.3 m, median 0.3 m). One nest was found behind a street sign. The nest interior was subdivided into many chambers with silk walls. Larvae and pupae were attached to the chamber walls by silk threads. The 13 nests were 4.0–26.0 cm wide (mean 8.9 cm, median 13.5 cm), 4.0–11.5 cm deep (mean 7.1 cm, median 7.5 cm) and 4.0–28.0 cm high (mean 14.0 cm, median 7.5 cm).

*P. (Myrmhopla) furcata* also constructs nests of silk reinforced by dead plant and soil particles. The nest shape was highly variable. Two nests resembled closely those ball-shaped nests of *P. dives*. These nests were located in the shrub layer, 1.73 m and 1.78 m above the ground. 13 nests, also constructed of silk combined with plant and soil matter, resembled irregularly shaped carton nests (Fig. 1F). These nests were built 2.1–3.2 m above the ground (mean 2.6 m, median 2.4 m). The material was woven very tightly. The nests were either flat and attached on the undersides of leaves or ball-shaped and fastened between two or three living leaves. Seven nests were located inside dry, rolled up leaves. The dry leaves had been spun together with a thin silk layer, the leaf surfaces inside the nests were lined with a silk layer. Many nests were subdivided into several chambers with silky walls. Larvae and pupae were attached to the nest walls by silk threads. 22 nests were measured. They were 6.5–26.0 cm wide (mean 14.0 cm, median 13.3 cm), 1.9–9.5 cm deep (mean 5.8 cm, median 6.0 cm) and 0.5–11.0 cm high (mean 3.7 cm, median 2.8 cm).

##### 4.2. Pure silk nests

*P. (Myrmhopla) bicolor* and *P. (Myrmhopla) muelleri* use larval silk to construct their nests in the vegetation (Jacobson, 1908; Karawajew, 1906; Dorow et al., 1990). The loosely woven and translucent nests of *P. muelleri* were mostly constructed without any detritus particles or contained very little particles of vegetative matter (Dorow et al., 1990). The nests were found in the shrub layer 1.2–4.2 m above the ground (mean 2.2 m, median 2.1 m). All nests consisted of oval silk webs attached to the lower surface of plants with large, broad leaves, mostly *Achasma* sp. (Zingiberaceae), but also *Donax grandis* (Maranthaceae), *Musa* sp. (Musaceae) *Citrus* sp. (Rutaceae) or palms (Palmae). So we found a greater variety of nest plants than originally assumed by Dorow et al. (1990). The 28 measured nests were 5.5–18.6 cm wide (mean 12.5 cm, median 12.8 cm), 3.2–11.0 cm deep (mean 5.9 cm, median 5.5 cm) and projecting beyond the lower leaf surface by 0.5–3.0 cm. Each nest consisted of a single chamber with one or two entrances. The leaf surface inside the nest was covered with a thin silk layer to which the white colored young larvae and the green colored last instar larvae and pupae were attached by silk threads.

The likewise well hidden silk nests of *P. bicolor* were located either between two or three relatively small leaves, e.g., of *Eugenia malaccensis* (Myrtaceae) or *Piper* sp. (Piperaceae), or between folded broad leaves, e.g., *Heliconia* sp. (Heliconiaceae), *Achasma* sp. (Zingiberaceae), *Citrus* sp. (Rutaceae) or palms (Palmae). The nests occur in many zones, from the shrub layer up to the forest canopy. The reachable nests were located 0.42–8 m above the ground. The leaves were spun together with a thin translucent layer of pure silk (Fig. 1E). The nests consisted of a single chamber with one to three entrances. The leaf surfaces inside the nests were covered with a thin silk layer to which the brood was attached. 39 nests were measured, they were 3.2–26.5 cm wide (mean 10.6 cm, median 10 cm), 1.3–13.1 cm deep (mean 5.6 cm, median 5.5 cm) and 0.5–6.3 cm high (mean 2.2 cm, median 1.5 cm).

### Colony structure

All investigated *Polyrhachis* species showed a polydomous colony structure, the colony members were distributed over several nests. The number of nests varied among the species. *P. muelleri* colonies, e.g., consisted of 1–3 nests (Table 2), *P. schellerichae* in contrast of 16–47 nests (Schellerich-Kaaden et al., 1997).

The number of queens also varied among the species (Table 2). In eight species we never found more than one dealate queen per colony, they seem to be monogynous. In *P. (Myrma) proxima*, two of the three investigated colonies also were monogynous, but the third one had two dealate queens. These two queens were located far apart from one another in different partial nests. In *P. (Myrmhopla) dives* we found one colony with two dealate queens in the same nest and two colonies with only one dealate queen. Yamauchi et al. (1987) counted on average 594 dealate queens per nest of *P. dives* in Okinawa but also reported a much bigger colony size.

The colony sizes varied considerably among the species (Table 2). *P. muelleri*, e.g., has very small colonies, with only 38–89 workers, while other species form large

**Table 2.** Number of nests per colony, number of dealate queens and number of workers per colony of 10 *Polyrhachis* species, sorted as in Table 1

Species	Number of nests	Number of dealate queens	Number of workers
<i>P. (Myrma) proxima</i>	3– 7 (n=3)	1–2	221–1422 (n=3)
<i>P. (Polyrhachis) bellicosa</i>	1– 4 (n=3)	1	14,425 (n=1)
<i>P. (Myrma) illaudata</i>	2– 6 (n=3)	1	348– 475 (n=3)
<i>P. (Myrma) nigropilosa</i>	5–17 (n=2)	1	249–1093 (n=2)
<i>P. (Myrmhopla) schellerichae</i>	6–47 (n=2)	1	2693–7203 (n=2) <sup>1</sup>
<i>P. (Myrmhopla) arachne</i>	2– 3 (n=2)	1	1176–4500 (n=2) <sup>2</sup>
<i>P. (Myrmhopla) dives</i>	2– 4 (n=3)	1–2 <sup>3</sup>	1003–2300 (n=2) <sup>4</sup>
<i>P. (Myrmhopla) furcata</i>	3– 8 (n=3)	1	1224–6418 (n=3)
<i>P. (Myrmhopla) bicolor</i>	8–13 (n=2)	1	406– 845 (n=2)
<i>P. (Myrmhopla) muelleri</i>	1– 3 (n=3)	1	38– 89 (n=3)

<sup>1</sup> Schellerich-Kaaden et al. (1997).

<sup>2</sup> Dorow et al. (1990); A. Schellerich-Kaaden (pers. com.).

<sup>3</sup> 594 queens (Yamauchi et al., 1987).

<sup>4</sup> 36,500 (Yamauchi et al., 1987).

colonies of more than 14,425 workers in one colony of *P. bellicosa*. Yamauchi et al. (1987) counted one colony of *P. dives* in Okinawa containing 36,500 workers. The colony comprised 63 nests in a study area of 750 m<sup>2</sup>. In West-Malaysia we only found smaller colonies (1003–2300 workers) with 2–4 nests but in Lombok (Indonesia) we observed *P. dives* colonies of similar sizes as in Okinawa. We did not investigate colony sizes in Lombok but in one case we counted 16 very large nests in an area of 160 m<sup>2</sup>. There might be an adaptive shift in social organisation of *P. dives* concerning polygyny and polydomy as it is known in species of *Iridomyrmex* and *Leptothorax* (Buschinger, 1968; Hölldobler and Carlin, 1985).

### *Nutrition habits*

In regard to the nutrition habits of the investigated *Polyrhachis* species we can distinguish two different major groups: Trophobiotic and non-trophobiotic species.

#### 1. Trophobiotic species

Four species of the subgenus *Myrmhopla* (*P. arachne*, *P. dives*, *P. furcata* and *P. schellerichae*) and one species of the subgenus *Polyrhachis* (*P. bellicosa*) keep trophobionts.

*P. arachne*, one of the bamboo specialists, and *P. dives* construct pavilions for their trophobiotic partners. The pavilions of both species were built of larval silk combined with debris and were located under leaf surfaces. *P. dives* guards trophobionts also outside the pavilions, even at night, when no foraging activity occurs. In case colonies of *P. arachne* inhabit living bamboo internodes, they often keep additional trophobionts inside these nests. *P. schellerichae* does not build pavilions. This bamboo specialist keeps its trophobionts exclusively inside the nest internodes.

Also *P. furcata* does not construct pavilions. The species is active 24 hours a day and guards its trophobiotic partners continuously. *P. (Polyrhachis) bellicosa*, in contrast, was observed to guard Coccidae outside the nests only during daytime.

*P. dives* and *P. furcata* were found with Aphidae, Coccidae, Pseudococcidae and Membracidae as trophobiotic partners. *P. arachne*, a bamboo specialist, tends Pseudococcidae and Aphidae in its pavilions and the pseudococcid *Kermicus wroughtoni* inside the bamboo internode. Like *P. arachne*, the second bamboo specialist *P. schellerichae* keeps *Kermicus wroughtoni* inside the nest internodes. Both species are able to regulate the density of their trophobionts. They carry trophobionts to other feeding sites (nests or, in the case of *P. arachne*, pavilions). We once observed *P. arachne* workers throwing living nymphs of *Kermicus wroughtoni* out of the nest.

#### 2. Non-trophobiotic species

Five species belong to this group (*P. bicolor*, *P. illaudata*, *P. muelleri*, *P. nigropilosa*, *P. proxima*). These species were never found together with trophobionts, but *P. proxima* and *P. illaudata* were observed collecting honeydew from the leaf surfaces, the other species take honey water solution in an experimental situation. When we



made the trophobionts of other ants available to these species, they did not exhibit any interest in them (no prolonged antennal contact).

*Polyrhachis* species also use other food resources, like floral or extrafloral nectaries, sugary saps of fruits and trees, food bodies, dead or living insect prey or electrolytes in form of vertebrate or bird excrement or urine (Table 3).

Nectaries were visited by some of the investigated *Polyrhachis* species. Even species with trophobionts like *P. furcata* and *P. bellicosa* were observed collecting food from floral nectaries of *Chasalia chartacea* (Rubiaceae). The plants with nectaries remained occupied by the ants for several weeks. *P. illaudata*, a non-trophobiotic species, visited the extrafloral nectaries of *Radermachera glandulosa* (Bignoniaceae) and *Macaranga tanarius* (Euphorbiaceae). This *Polyrhachis* species does not monopolize the nectaries, other ant species were able to frequent them at the same time. *P. nuelleri* fed on nectaries of *Macaranga tanarius* in an experimental situation.

Sugary saps of fruits were collected by *P. bicolor* on a fruiting water apple tree (*Eugenia malaccensis*, Myrtaceae). *P. nigropilosa* was observed collecting sugary saps from the bark of a fallen tree.

Food bodies of *Cayratia japonica* and *C. mollissima* (Ampelidaceae) were offered to *P. bellicosa*, *P. bicolor*, *P. dives* and *P. illaudata* in the laboratory. All these species collected the food bodies and carried them into their nests.

When sphingid and tortricid larvae were offered to *P. bellicosa*, *P. bicolor* (Rabenstein, 1995), *P. furcata* and *P. schellerichae* they bit these prey objects and carried them to their nests. In the laboratory *P. dives* captured brachypterous *Drosophila* specimens.

### Foraging periods

*P. (Myrmhopla) furcata* was active for 24 hours. *P. (Myrma) nigropilosa* was only active during night. *P. (Myrma) illaudata* was sometimes foraging after dark, but was predominantly diurnal. All other investigated species were only active at day time.

**Table 3.** Food resources of 10 *Polyrhachis* species, sorted as in Table 1

Species	Trophobionts	Nectaries/sugary saps <sup>1</sup>	Honey water	Dead insect prey	Living insects	Electrolytes <sup>2</sup>
<i>P. (Myrma) proxima</i>	—	+	+	+	—	+
<i>P. (Polyrhachis) bellicosa</i>	+	+	+	+	+	+
<i>P. (Myrma) illaudata</i>	—	+	+	+	—	+
<i>P. (Myrma) nigropilosa</i>	?	+	+	+	—	+
<i>P. (Myrmhopla) schellerichae</i>	+	—	+	+	+	+
<i>P. (Myrmhopla) arachne</i>	+	—	+	+	+	+
<i>P. (Myrmhopla) dives</i>	+	—	+	+	+	+
<i>P. (Myrmhopla) furcata</i>	+	+	+	+	+	+
<i>P. (Myrmhopla) bicolor</i>	—	+	+	+	+	+
<i>P. (Myrmhopla) muelleri</i>	—	+	+	+	—	+

<sup>1</sup> Sugary excrement of scale insects on the leaf surfaces, sugary saps of fruits and trees.

<sup>2</sup> Vertebrate excrement or urine.

\* Observed without experimental manipulations.

### Food recruitment

All recruitment systems known from ants (Hölldobler and Wilson, 1990) were found in *Polyrhachis*. A detailed signal analysis is in preparation by Liefke et al.

*P. proxima* employs "tandem running". This system is characterized by one nestmate following the successful scout in close antennal contact. The nocturnal *P. nigropilosa* uses "group recruitment". One, two or three recruited ants at a time follow closely behind a leader ant to the target area. The leaders lay chemical trails on their ways home and back to the target. *P. illaudata* also employs "group recruitment". The scouts use tactile signals inside the nest to recruit nestmates and lay chemical trails between nest and target. Usually a scout guides a small group of nestmates to the food, but stimulated nestmates are also able to follow the chemical trail without a leader.

*P. arachne*, *P. bicolor*, *P. muelleri* and *P. schellerichae* likewise use tactile stimulation inside the nest. The trail pheromone alone has no sufficient recruitment effect. In these four species we observed the following interactions between the initial recruiter and her nestmates after mechanical invitation: 1) the scout remained for some time inside the nest performing motor displays while nestmates left the nest to follow the trail, 2) the recruited nestmates overtook the scout on its way back to the food source and continued to follow the trail, 3) the scout returned quickly to the food area and the recruited ants followed closely behind.

The modes of recruitment employed by *P. bellicosa*, *P. dives* and *P. furcata* are similar. Tactile stimulations by recruiting ants were involved, but we also noticed that workers can follow the chemical trails even though they were not first mechanically stimulated. The system can be classified as "mass recruitment".

### Discussion

For the Neotropics it has been proposed that niche differentiation and interspecific competition are important parameters in structuring ant communities (Wilson, 1987; Linsenmair, 1990). Investigations on the diversity of the ponerine ant genus *Leptogenys* in Peninsular Malaysia led to similar conclusions (Maschwitz et al., 1989; Steghaus-Kovac and Maschwitz, 1993). All investigated *Leptogenys* species exhibit similar life habits: they live on the ground, do not construct nests and are strictly carnivorous. But pronounced differences occur in the mode of hunting and in the degree of prey specialization. Wilson (1987) suggested that in arboreal ants, in contrast, the nest site differentiation among species may be an important niche parameter.

We analyzed the nesting resources of 10 syntopic *Polyrhachis* species. These species differ remarkably in their nesting habits and exhibit different nest site specializations:

#### 1. More or less independence of environmental prerequisites

*P. (Myrma) proxima* digs its nests in the soil and is therefore independent of preformed cavities. *P. (Myrmhopla) furcata* and *P. (Myrmhopla) dives* construct silk

nests reinforced by dead vegetative and soil particles. Similar nesting habits were found in 13 species of *Camponotus* subgenus *Karavaivia* (Maschwitz et al., 1985; Dumpert et al., 1989, 1995). The *Karavaivia* species produce silk pavilion nests. Earth particles, detritus and bits of plants are inserted into the silk layer. However, most of these nests are built onto the underside of leaves. But there are also species constructing nests between leaves like *Camponotus* (*K.*) *texens* and *C. (K.) orinus*. The two *Polyrhachis* species, in contrast, are more variable and use a wide range of environmental structures to attach their nests. They resemble very much the flexible nesting habits of the Australian species *Polyrhachis* (*Cyrtomyrma*) near *doddi*, as described by Hölldobler and Wilson (1983). Thus, in *P. dives* and *P. furcata* there exist no limitation of nesting sites above the ground. Only *P. dives* has been found to nest also directly on the ground.

*P. (Polyrhachis) bellicosa* constructs its nests between grass and shrubs or between dry leaves. This species needs stalks of grass or shrubs to prop up its nests which are built of dead plant and soil particles without silk supplement. *P. bellicosa* therefore is more dependent on structures as the former species.

## 2. Specialization on preformed cavities

The cavity nesters show different types of nesting specializations. *P. illaudata* and *P. nigropilosa* use a variety of cavity types. *P. schellerichae* and *P. arachne*, in contrast, nest only in bamboo internodes. Both species show a specialization on giant bamboo species (Dorow and Maschwitz, 1990; Schellerich-Kaaden et al., 1997). *P. schellerichae* does not use silk for nest modification and is restricted to bamboo internodes with small openings. *P. arachne*, in contrast, is more variable. The ants use silk combined with debris to close big openings and to construct pavilions under the leaf surfaces for their trophobionts. Moreover *P. schellerichae* is restricted to living stems whereas *P. arachne* uses also standing dead bamboo culms.

## 3. Specialization on leaves and on particular leaf positions

*P. (Myrmhopla) bicolor* and *P. (Myrmhopla) muelleri* construct pure silk nests in the vegetation. Unlike *Oecophylla* spp., which create natural enclosures for their pure silk nests by pulling leaves together (Doflein, 1905), the two *Polyrhachis* species choose locations on plants with suitable leaf positions. *P. muelleri* is found mainly on broad-leaved plants. *P. bicolor*, in contrast, constructs its nests between smaller leaves or between broad folded leaves. Thus, the nesting sites of these two ant species do not overlap.

## *Silk nest weaving*

Silk nest construction is known to occur in at least 264 *Polyrhachis* spp., i.e., a considerable majority of the 460 known representatives of the genus (Dorow, 1995). The known silk nest weavers belong to 8 out of the 12 subgenera (among them *Myrmhopla*). In three subgenera (including the subgenus *Polyrhachis*) no silk nest builders are found. In one subgenus, *Myrma* (109 spp.), both silk nest weavers and

non-weaving species occur (Dorow, 1995). These as well as our findings suggest that silk nest weaving increases the nest diversity in the genus *Polyrhachis*.

As natural preformed nesting sites are rather limited in the canopy region of the forest, weaver ant species are more or less free from the spatial limitations imposed on species that must live in preformed vegetative cavities. Baroni Urbani (1989) pointed out, that nesting behavior, colony size and food preference appear to have been selected several times within the ants by similar ecological pressure. Silk nest construction by using larval silk, for instance, has evolved at least 5 times within the Formicinae (Hölldobler and Wilson, 1983; Maschwitz et al., 1985). Some non weaving species also use the advantages of silk nests by incorporating spider silk in their nests like *Polyrhachis laboriosa* (Collart, 1932).

Dwyer and Ebert (1994) reported the use of spider silk in two weaving *Polyrhachis* species (*P. (Cyrtomyrma) doddi* and *P. (Cyrtomyrma) pilosa*) in the initiation of nest building or the extension of nests. As we did not check nest building activity in our study we can not elucidate this point for the investigated species.

### *Colony structure*

The colony sizes of *Polyrhachis* spp. vary considerably. But all investigated species, even those with very small colonies, are polydomous. Like all social insects, ants are central place foragers (Hölldobler and Wilson, 1990); this means, a forager retrieves the food to the nest and therefore has to travel greater distances than if she could rest anywhere. A polydomous colony structure reduces the distances between foraging sites and the nearest nest (Hölldobler and Lumsden, 1980). Polydomous species housing trophobionts can minimize the distances also to their trophobiotic partners and are able to guard and defend the trophobionts more effectively. Moreover, scavenging in large areas is more efficient when the nests are decentralized.

### *Nutrition habits, recruitment systems and colony size*

None of the investigated species shows any pronounced specialization in regard to protein resources. Whereas four of the investigated species are mainly scavengers, the six remaining species exhibit at least some solitary hunting behavior on small prey objects. The African species *P. laboriosa* and *P. militaris* also capture prey by solitary hunting (Dejean et al., 1994; Lenoir and Dejean, 1994).

For obtaining carbohydrates one group of species monopolizes trophobionts. The trophobionts are kept inside the nest, inside pavilions, openly exposed and guarded or not guarded by the workers. The second group exploits sugar sources opportunistically, but never obtains honeydew from trophobionts by an interspecific communication act. The first group is characterized by large, the second by small colonies. All species of the first group use efficient recruitment systems. *P. arachne* and *P. schellerichae* employ tactile stimulations inside the nest but a leader ant is not necessary. The recruitment system resembles the recruitment system of *Formica fusca* (Möglich and Hölldobler, 1975). The recruitment behavior of *P. bellicosa*, *P. dives* and *P. furcata* can be classified as "mass recruitment" (Wilson, 1962). These

findings suggested that colony size to some extent is correlated with the food recruitment system (Beckers et al., 1989). Two of the species, *P. dives* and *P. furcata*, defend rich sugar sources, like trophobionts or plants with nectaries. These species are able to occupy territories to a certain extent. One *P. furcata* colony was observed to defend its territory against the highly dominant *Oecophylla smaragdina*. In another case we observed *P. dives* being displaced from its territory by a dominant *Camponotus* species. Dejean et al. (1994) made similar observations with *P. laboriosa*, a non-dominant arboreal ant of the African equatorial forest, which is sometimes able to occupy territories in the manner of dominant ants.

*P. bellicosa* forms trunk trails in an area of at least 400 m<sup>2</sup>. In one case the ants were found in the same area over a period of three years. The bamboo specialists *P. arachne* and *P. schellerichae* avoid fights with other ants. In competitive interactions over food between these two species, *P. arachne* is superior. Workers of *P. schellerichae* have cryptic habits and most of the time they stay with the trophobionts inside the nests despite their very large colonies (up to 7203 members, Schellerich-Kaaden et al., 1997).

The five species of the second group (*P. bicolor*, *P. illaudata*, *P. muelleri*, *P. nigropilosa* and *P. proxima*) have considerably smaller colonies (between 40 and 1500 workers). All these species are non-dominants (sensu Majer, 1972) and do not occupy territories. Of these, *P. proxima* uses "tandem running" and *P. nigropilosa* "group recruitment". In these species only small groups of workers were recruited. Both recruitment patterns are well known within the Formicinae. Hölldobler et al. (1974) described tandem running in *Camponotus sericeus*. Group recruitment is known from *Camponotus socius* (Hölldobler, 1971), *C. paria* and *C. compressus* (Hingston, 1929). *P. illaudata* also employs "group recruitment" but nestmates are able to follow a chemical trail without a leader. In situations of direct competition with other ant species *P. proxima*, *P. nigropilosa* and *P. illaudata* are usually subordinate and not able to defend the food. *P. bicolor* and *P. muelleri* use the same recruitment system as *P. arachne* and *P. schellerichae*: tactile stimulation inside the nest but a leader ant is not necessary. However, *P. bicolor* and *P. muelleri* have small colonies and are therefore not able to recruit many nestmates. In competitive situations both species are subordinate. Their nests are not very durable and, in consequence, colonies have to relocate frequently. The recruitment systems of *P. bicolor* and *P. muelleri* may therefore be more important for colony emigrations than for foraging.

The majority of *Polyrhachis* species is active during day time. Of the studied species only *P. nigropilosa* is nocturnal and can coexist with the diurnal *P. arachne* in the same habitat (in bamboo stands) without ever competing directly for food. Of course there are many other nocturnal ant species. In confrontation with those (e.g., *Camponotus gigas*), *P. nigropilosa* is subordinate and not able to defend food sites.

At the beginning we pointed out that carnivorous ants of the ponerine genus *Leptogenys* show pronounced differences in dietary but not in nest site specialization (Maschwitz et al., 1989). In *Polyrhachis*, in contrast, we found considerable specializations in nesting requirements. In regard to the nutrition habits two major strategies were found: trophobiotic and non-trophobiotic species. The trophobiotic species keep their trophobionts inside the nest, inside pavilions, openly exposed and guarded or not guarded by the workers. The differences in nutrition habits of the ten investigated species are closely connected with many other biological features

as colony size, recruitment system or territorial defence. Thus nesting habits as well as nutrition habits seems to be key factors allowing the coexistence of so many different *Polyrhachis* species.

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